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Only sun-lit leaves of the uppermost canopy exceed both air temperature and photosynthetic thermal optima in a wet tropical forest

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ABSTRACT

Tropical forests have evolved under relatively narrow temperature regimes, and therefore may be more susceptible to climatic change than forests in higher latitudes. Recent evidence shows that lowland tropical forest canopies may already be exceeding thermal maxima for photosynthesis. Height can strongly influence both the microclimate and physiology of forest canopy foliage, yet vertical trends in canopy micrometeorology are rarely examined in tropical forests. To improve our understanding of how climatological and micrometeorological conditions affect tropical tree function, we assessed vertical gradients of photosynthetic photon flux density, vapor pressure deficit, air temperature, leaf temperature, and the difference between leaf and air temperature (ΔT) in a Puerto Rican tropical wet forest. Both air temperature and vapor pressure deficit increased linearly with height. Leaf temperature, however, did not significantly differ across the shaded foliage from 0-16 m, while the uppermost layer (20 m) was up to 4°C hotter than the rest of the foliage and up to 5°C hotter than air temperature at the highest radiation intensity. As a result, leaf temperatures in the shaded middle canopy and understory showed nearly poikilothermic behavior (i.e., leaf temperatures = air temperature), while the uppermost canopy strata showed megathermic behavior (i.e., leaf temperatures greater than air temperature), revealing different thermoregulation strategies for sun-lit versus shaded foliage. In addition, the uppermost canopy was the only stratum to exceed mean photosynthetic temperature optima for this site (T_{opt} = 30.2 ± 1.1°C). Because the upper canopy plays a disproportionately large role in whole-forest photosynthesis, continued warming could potentially weaken the tropics' carbon sink capacity. However, the shaded leaves may be able increase carbon uptake with further warming because they appear to be able to maintain temperatures below photosynthetic optima, possibly with the help of radiation shielding provided by the uppermost canopy layer.

1. Introduction

Tropical forests play a critical role in global carbon sequestration because they contain more aboveground biomass and exchange more carbon dioxide (CO_2) with the atmosphere than any other terrestrial biome (Beer et al., 2010; Pan et al., 2013). Tropical ecosystems have evolved under very narrow climatic envelopes, and these temperature ranges are expected to shift dramatically within the next decade due to anthropogenic climate change (Diffenbaugh and Scherer, 2011). Furthermore, because tropical ecosystems have not evolved under a broad range of climate regimes, tropical plants may have less capacity to physiologically acclimate to a changing climate than plants from higher latitudes, where temperatures vary more across seasons and years (Cunningham and Read, 2003). A recent global analysis suggests that physiological safety margins of forest canopies in all latitudes could become even more narrow with continued warming and more frequent heat waves (O'Sullivan et al. 2017). Altogether, evidence points to a declined capacity for tropical forests to sequester atmospheric carbon in a warming world.

Photosynthesis has a unimodal response to temperature, where CO_2 assimilation declines if a plant is experiencing temperatures higher than the optimum temperature (T_{opt}). Increasing temperatures can indirectly cause photosynthetic decline as a result of concurrent increases in vapor pressure deficit (VPD), which induce stomatal closure (Lloyd and

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Farquhar, 2008). Temperature can also result in declines of photosynthesis above the optimum temperature through direct effects on enzyme behavior, diffusion rates, or thylakoid membrane function (Lloyd and Farquhar, 2008). Whether or not foliage is operating above or below this optimum photosynthetic temperature often depends on where the leaves are located within the vertical canopy gradient. Leaves in closed-canopy evergreen tropical forests primarily exist in two distinct states: brightly illuminated or very shaded (Doughty and Goulden, 2008). Sun leaves operate close to threshold temperatures for photosynthetic production (Mau et al., 2018), and further warming could result in decreased carbon uptake or even permanent damage (Doughty, 2011). Tropical forests are already operating closer to their optimum temperatures compared to temperate and boreal sites around the globe (Huang et al. 2019). Decreased photosynthetic productivity can cause declines in gross primary production (GPP), making these forests weaker carbon sinks, and possibly net sources of carbon to the atmosphere which may create a positive feedback loop and thus exacerbate further climate warming (Doughty and Goulden, 2008).

Much of the research on forest microclimates has focused on changes through time or across horizontal space (e.g., Brown 1993; Wang et al. 2003), or localized micrometeorology differences due to disturbances (Fetcher et al., 1985; Jucker et al., 2018; dos Santos et al., 2020; Hardwick et al., 2015). Microclimate can also vary greatly across vertical canopy gradients. In closed-canopy forests, upper canopies generally exhibit higher leaf and air temperatures, greater turbulence, lower humidity, and higher light than the more shaded canopy and understory (Rey-Sánchez et al., 2016; Mau et al., 2018; Doughty & Goulden 2008, Stiegel et al. 2017). Open-grown trees, on the other hand, can show little vertical temperature variation (Zweineicki et al. 2004) or even higher temperature in the lower canopy, for example, in desert tree species (Curtis et al. 2019). While most canopy process models use air temperature from meteorological stations to drive physiological function (Blum et al. 2013), leaf temperatures are more directly correlated to stomatal closure than air temperatures are (Koch et al. 1994). Stomatal behavior directly affects photosynthesis and ultimately forest carbon uptake, yet few studies have investigated how both leaf temperature and air temperature change across a canopy height gradient in closed-canopy tropical forests (Fauset et al., 2018; Rey-Sánchez et al., 2016). Vertical variation in physiological function is driven by vertical variation of microclimate in tropical canopies, including photosynthetic capacity, foliar respiration, leaf mass per area, foliar chemistry, and woody respiration (Cavaleri et al., 2008, 2006, 2010; Meir et al., 2002; Weerasinghe et al., 2014). Spatially accurate measurements of leaf temperature also allow for more accurate modeling of whole-plant transpiration (Bauerle et al., 2009). Thus, examining vertical variation in canopy microclimate would greatly improve our understanding, representation, and simulation of both water and carbon fluxes at the plant and forest scale.

The primary objective of this study was to assess the spatial and temporal variability of microclimatic variables along a vertical gradient of a tropical wet forest canopy. We hypothesized that: 1) both leaf temperature (T_{leaf}) and air temperature (T_{air}) would increase with canopy height, but at different rates such that 2) the difference between leaf and air temperature (ΔT) would also increase with canopy height due to effects of increasing solar radiation. We also expected 3) the upper canopy T_{leaf} to exceed photosynthetic thermal optima (T_{opt}) for at least part of the day.

2. Materials and Methods

2.1. Study site

Microclimatic data were collected from a canopy access tower at the USDA Forest Service Sabana Field Research Station in the Luquillo Experimental Forest located in Luquillo, Puerto Rico (18°18'N, 65°50'W). The walk-up aluminum tower had eleven 1.8 m tall sections, for a total of ~20 m in height (UpRight Inc., Dublin, Ireland). The site is: 100 m in elevation, with mean annual temperature of 24 °C, mean annual rainfall of 3500 mm, and Utisol soil (Kimball et al., 2018). The forest is classified as a subtropical wet forest (Holdridge, 1947). The stand structure of the forest was 3100 trees per hectare with 38.76 m^2 ha^{-1} of basal area (data not shown).

2.2. Study design and micrometeorological instrumentation

The micrometeorology data were collected with solar shielded air temperature and humidity sensors (HOBO, Onset Corp, Bourne MA) paired with infrared temperature sensors and a datalogger (SI-100, Apogee Instruments, Logan UT and CR800, Campbell Scientific, Logan UT) aimed at clusters of leaves adjacent to the tower at a distance of approximately 45 cm from each sensor. Six pairs of sensors were placed at heights of 2, 6, 9, 12, 16, and 20 meters (two sensors at each height; Figure 1). Some of the sensors had to be placed at heights within half a meter up or down from their partner sensor to account for leaf locations, but height values were rounded to the nearest meter, and the 20 m sensors represent the top of the canopy. Species varied by height, and multiple species were captured at some heights, but the primary species measured by the leaf temperature sensors were the two canopy tree species *Guarea guidona and Ocotea sintenisii*, and the palm *Prestoea montana*. Photosynthetic photon flux density (PPFD) was measured at the top (20 m) and middle (10 m) of the tower (Figure 1) with photosynthetically active radiation (PAR) sensors and dataloggers (HOBO S-LIA-M003 and HOBO Microstation H21, Onset Corp, Bourne MA). All meteorological data were sampled every two minutes and averaged over a half-hourly period. Vapor pressure deficit (VPD) was calculated using air temperature and relative humidity as described in Murray (1967). Air temperature and humidity sensors recorded data from May 19th to July 6th, 2017 except for one 12-meter sensor which recorded only from May 19th to June 5th, 2017 (due to sensor malfunction). Leaf temperature sensors recorded from May 18th to July 6th, 2017. PPFD was collected at 10 m from May 19th to June 5th, 2017 and at 20 m the data were collected from May 18th to July 6th 2017. Start and stop dates varied slightly due to tower installation logistics.

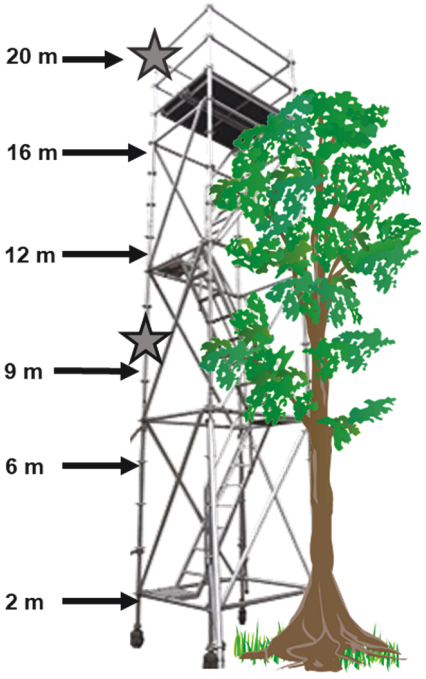

Figure 1. Locations of sensors on the canopy access tower, arrows indicate the temperature and humidity sensors (n=2), while stars indicate photosynthetically active radiation (PAR) sensors.

2.3. Photosynthetic temperature optimum

To investigate whether foliage temperatures exceeded optimum temperatures of photosynthesis (T_{opt}), we compared T_{leaf} data with photosynthetic temperature response curves of shrub, tree, and liana species accessible across the vertical gradient of the canopy access tower measured in May 2016. We used a LI6400XT infrared gas analyzer with the 6 cm^2 leaf chamber (6400-02B, Li-COR Inc., Lincoln, NE, USA) to measure light-saturated photosynthesis at 23, 25, 30, 33, 35, 37, and 40°C on leaves still attached to the branch. Light saturation was determined at each canopy level prior to the temperature response curves: 800 μmol m^{-2} s^{-1} from 0-12.6 m and 1000 μmol m^{-2} s^{-1} from 14.4-20 m. Leaf temperature was controlled by using gravity to pull hot or cold water through the Expanded Temperature Control Kit (6400-88, Li-COR Inc.), and measured inside the leaf chamber with a built-in thermocouple. Flow rate was controlled between 100-400 μmol m^{-2} s^{-1} to keep VPD between 1 and 2.5 kPa; although, VPD occasionally rose above 3 kPa at high temperatures. Chamber CO_2 was controlled at 400 ppm. Two understory shrubs (*Psychotria brachiata* and *Miconia prasina*), a palm tree (*Prestoea montana*), an unidentified liana species, and two canopy tree species (*Guarea guidonia* and *Ocotea sintenisii)*, were sampled. Number of measurements per species ranged from 1-7, depending on how many heights per species were accessible from the tower or from the ground. T_{opt} for each temperature curve was estimated using June et al. (2004):

$$A_{net} = A_{opt} \times e^{-\left(\frac{T_{leaf} - T_{opt}}{\Omega}\right)} \quad (1)$$

A_{net} is the net assimilation rate at the leaf temperature (T_{leaf}), A_{opt} is the rate of photosynthesis at the optimum temperature, and Ω is the difference in T_{opt} and the temperature where A_{net} drops to 37% of A_{opt}, often referred to as the thermal breadth of photosynthesis or the width of the temperature curve.

2.4. Data analysis

The diurnal cycles were displayed using half-hourly averages of each variable and applying 95% confidence intervals. Height categorizations were determined qualitatively, where 'upper' described highly exposed sun leaves in the uppermost tower section (20 m), 'middle' described foliage of mature trees and saplings in the shaded mid-canopy (6 – 16 m), and 'understory' was foliage of seedlings and saplings accessed from the ground (0-2 m). A bivariate linear regression was used on all species pooled to assess whether T_{opt} changed with canopy height, as there were not enough heights accessible from the tower for individual species to explore within-species height variation. Daily daytime averages and daily maxima of all half-hourly daytime values were calculated for each meteorological variable (ΔT, T_{leaf}, T_{air}, VPD, PPFD). The differences between daytime measurements of leaf temperature and the corresponding air temperature were expressed as ΔT for each half-hourly increment. We used Analysis of variance (ANOVA) procedures and Tukey's honest significant difference post-hoc mean separation to determine differences across canopy height class for the measured values of: PPFD, T_{leaf}, T_{air}, and VPD. Analysis of covariance (ANCOVA) procedures were used to assess leaf temperature response to air temperature for all canopy positions (understory, middle, upper). Additional ANCOVAS were used to assess T_{leaf} and ΔT responses to PPFD for middle and upper canopy positions. We used a student's t-test to determine if ΔT was statistically different from 0°C. All statistical analyses were performed in R (Version 3.5.1, The R Foundation for Statistical Computing).

3. Results

3.1. Variation in canopy micrometeorological variables across time and space

Diurnal patterns of leaf temperature (T_{leaf}) and the difference between T_{leaf} and T_{air} (ΔT) were quite different in the uppermost canopy strata (20 m) compared to the rest of the vertical gradient. ΔT showed the greatest diurnal variation in the upper canopy, where ΔT was lowest at night and greatest at midday (Figure 2a). Foliage in the lower canopy strata was apparently more buffered against diurnal temperature fluctuations. Air temperature (T_{air}) and VPD showed similar diurnal patterns across all heights, with gradual increases with height and midday peaks (Figures 2c, e). In contrast, T_{leaf} was not significantly different across canopy heights from 0-16 m (i.e., understory and middle canopy), but at the very top of the 20 m canopy (i.e., upper canopy), average leaf temperatures were ~3°C higher at midday compared to the mid canopy and understory (Figure 2b). Photosynthetic photon flux density (PPFD) also differed dramatically between upper and middle canopy sampling positions, with upper canopy peaking nearly 1000 μmol m^{-2} s^{-1} higher in the upper canopy foliage (20 m) compared to the middle canopy (10 m; Figure 2d).

Averages of daily mean and peak values across the vertical gradient show similar patterns to those revealed by diurnal traces, with abrupt changes in leaf temperatures and radiation in the upper canopy and a more gradual vertical increase of air temperature and VPD. Mean daily ΔT was actually negative in the middle canopy and the understory, whereas it was positive only in the upper canopy (Figure 3a). Maximum daily ΔT increased with increasing canopy position, and all positions showed positive maximum values (Figure 3b). Daily average and maximum daytime T_{leaf} did not differ between understory and middle canopy and were greater in the upper canopy for both variables (Figures 3c-d). Both T_{air} and VPD increased with height as well, but the increases were more gradual and not as abrupt as in the T_{leaf} gradient (Figures 3e-f, i-j). Mean daily daytime PPFD in the upper canopy was ~800 μmol m^{-2} s^{-1} greater in the upper vs. middle canopy, and peak daily PPFD was over 1000 μmol m^{-2} s^{-1} greater in the upper canopy (Figures 3g-h).

When comparing T_{leaf} and T_{air} directly, a pattern of leaf thermoregulation emerged which was distinct in the upper canopy. T_{leaf} was no different than T_{air} in the understory or the mid canopy ($p < 0.001$). However, in the upper canopy mean daily T_{leaf} is was 0.67°C higher than T_{air} ($p < 0.001$), and maximum daily T_{leaf} was 2.7°C higher than T_{air} ($p < 0.001$). The slope of the leaf temperature versus air temperature relationship fell on the 1:1 line in both the understory and mid canopy, while the slope in the upper canopy was significantly steeper (ANCOVA interaction: $p < 0.001$) (Figure 4). Thus, leaf temperature was only greater than air temperature in the upper canopy.

3.2. Effects of radiation on leaf thermoregulation

The pattern in light intensity differed drastically between upper and mid canopy. The daily daytime means and daily maximum values of PPFD were significantly greater in the upper canopy compared to the middle canopy (Figure 2d, 3g-h). The responses of T_{leaf} and ΔT to photosynthetically active radiation were significantly different among the canopy positions as well. ANCOVA analyses revealed significant interactions ($p < 0.001$ for T_{leaf}; $p < 0.001$ for ΔT), where both T_{leaf} and ΔT showed much higher temperature responses to light in the upper canopy compared to the middle canopy, in addition to exposure to greater light intensity maxima (Figure 5). These comparisons should be interpreted with caution, however, because middle canopy PPFD did not exceed 1500 μmol m^{-2} s^{-1}, and therefore the difference in slopes cannot be extrapolated beyond this light level.

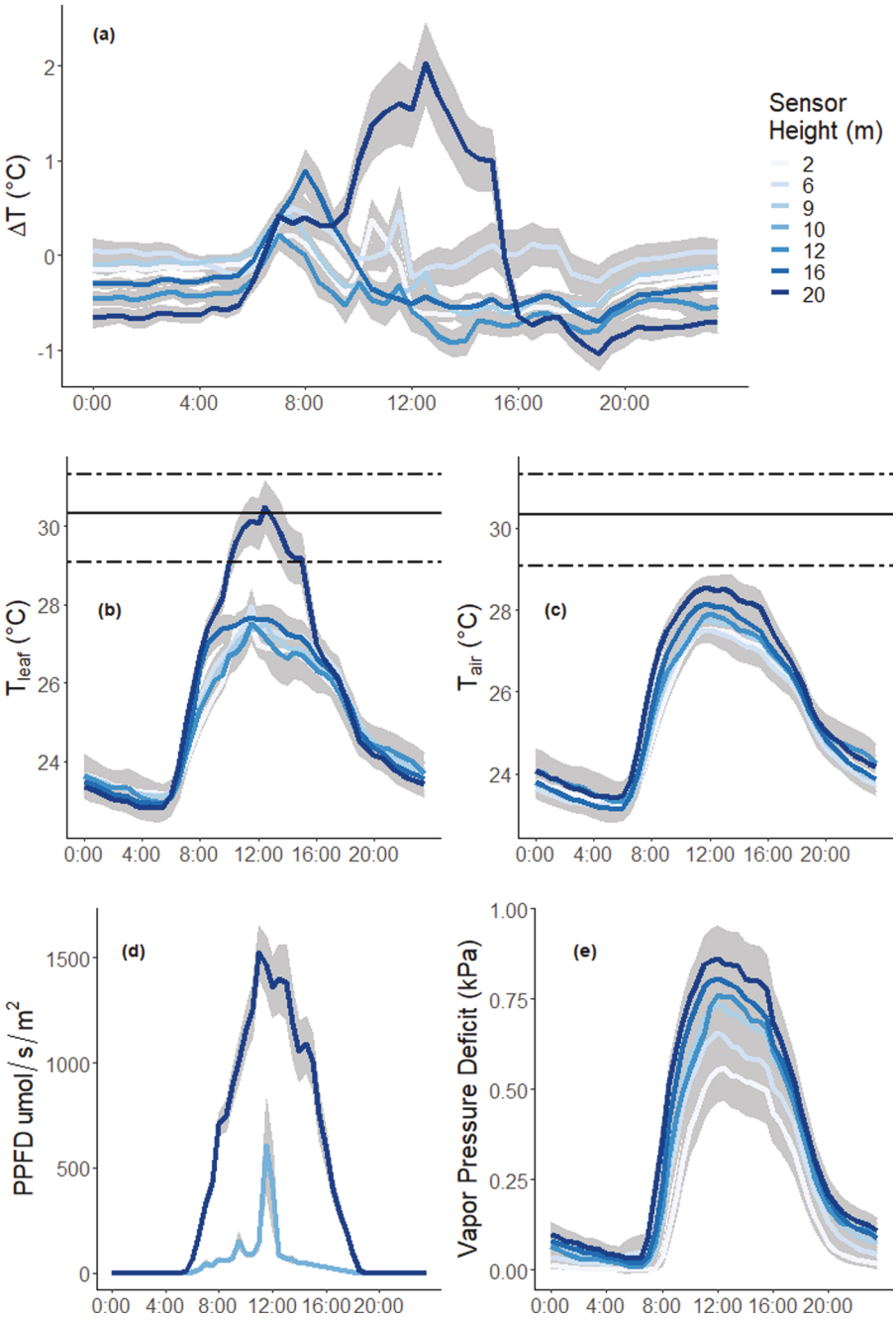

Figure 2. Diurnal patterns of micrometeorological variables from multiple sensor heights across the vertical canopy gradient. Panels represent diurnal patterns of (a) the difference between leaf and air temperature, (b) leaf temperature, (c) air temperature, (d) vapor pressure deficit, and (e) photosynthetic photon flux density. Shading indicates 95% confidence intervals around the averaged half hourly values. Solid and broken horizontal lines indicate mean and 95% confidence interval, respectively for thermal optimum temperature for photosynthesis of this site (T_{opt} = 30.2 ± 1.1°C). Shades of blue represent the heights measured along the canopy profile (2-20 m).

3.3. Comparison of leaf temperatures with photosynthetic optima

Leaf temperatures exceeded photosynthetic optima only in the upper canopy, and only at midday. Mean photosynthetic T_{opt} pooled across all species accessible from the tower was 30.2 ± 1.1°C (mean ± 95 %CI) and did not vary with canopy height ($p = 0.783$; Figure 6). T_{leaf} exceeded T_{opt} in the upper canopy at midday, but the foliage from all the rest of the canopy layers remained below T_{opt} for the entire day (Figure 2b). On average, upper canopy leaves spent approximately 0.5 hours per day at temperatures above T_{opt} (Figure 2b). On the days where temperatures did exceed T_{opt} (34 of 50 days, or 68% of days), the average amount of time spent at temperatures exceeding T_{opt} was 3.4 (±0.4) hours.

4. Discussion

4.1. Vertical gradients of micrometeorology and leaf temperatures

We found a dramatic difference between leaf temperatures in the very top layer of leaves compared to the rest of the canopy. In particular, while air temperature increased steadily and linearly with height, T_{leaf} in the understory and middle canopy layers (0-16 m) of this tropical forest were similar to each other and notably lower than for the upper canopy (20 m; Figure 2). Rey-Sánchez et al. (2016) found that T_{leaf} increased linearly with height during the wet season of a semi-deciduous tropical forest in Panama, whereas T_{leaf} was uniform throughout the canopy during the dry season. Mau et al. (2018) also found linear increases in T_{leaf} with height in both tropical moist and tropical wet forests in Puerto Rico. In contrast, we found little to no T_{leaf} variation in the understory and middle canopy, while the upper canopy mean daily T_{leaf} values were

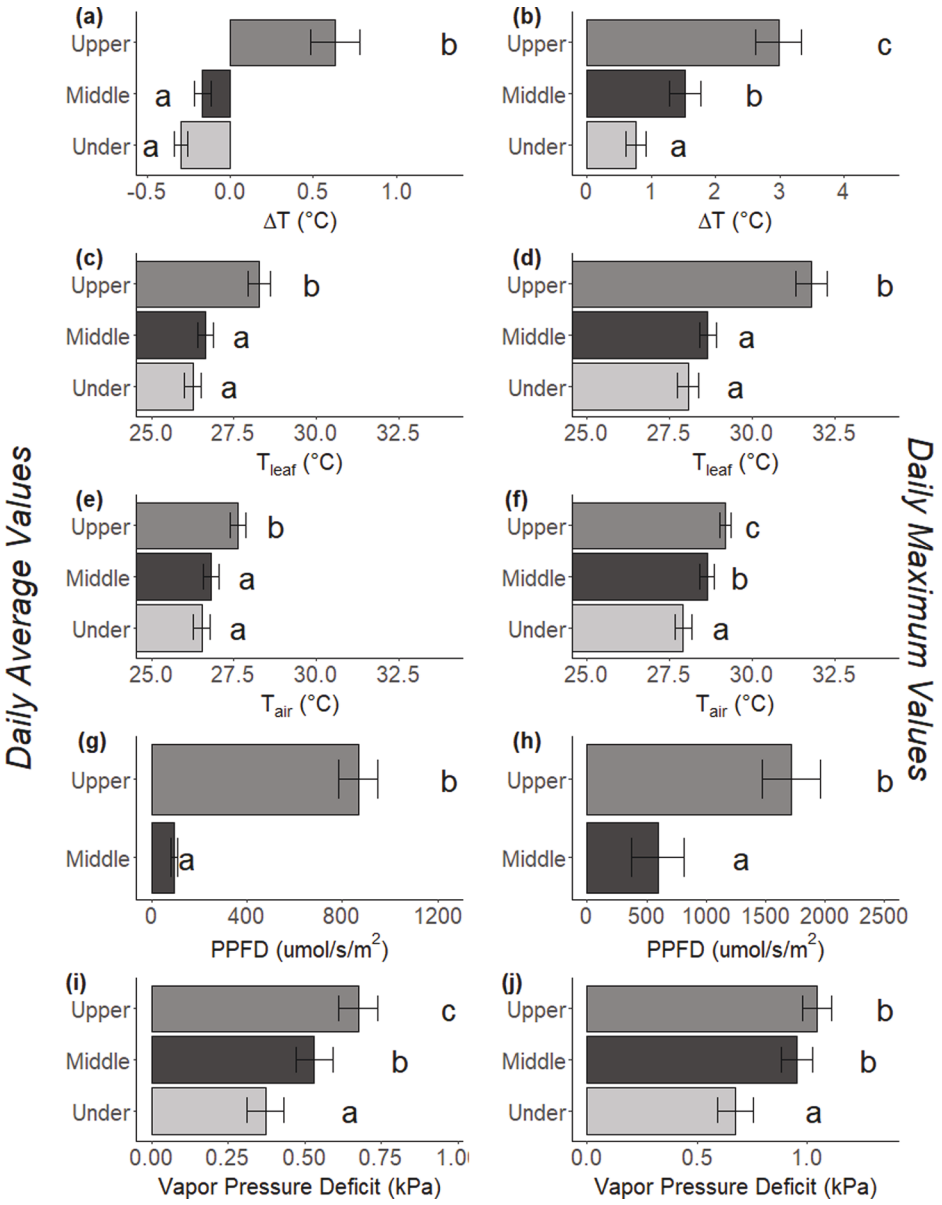

Figure 3. The daytime averages and maximums of (a-b) the difference between leaf and air temperature, (c-d) leaf temperature, (e-f) air temperature, (g-h) photosynthetic photon flux density, and (i-j) vapor pressure deficit in the upper canopy (20 m), middle canopy (6-16 m), and understory (0-2 m). Error bars indicate 95 % confidence intervals. Tukey's honest significance difference post-hoc results are displayed as letters where different lowercase letters represent significant differences among canopy locations.

~2°C higher, and maximum daily T_{leaf} values were ~4°C higher than the entire rest of the canopy. The jump in T_{leaf} at the highest canopy position in our study seems to be driven by the large difference in solar radiation above versus below the uppermost canopy strata (Figure 6a,b). Similar to other studies (e.g., Barker 1996), PPFD drastically declined between the upper canopy and the lower canopy, with a difference frequently greater than 1000 umol m^{-2} s^{-1} across ten vertical meters (Figure 2). Our results add to the growing evidence of the disconnect in forest canopies between T_{air} and T_{leaf} and support the notion that T_{air} is not an appropriate proxy for T_{leaf} of sun leaves in tropical forest ecosystem process models (Doughty & Goulden 2008; Rey-Sánchez et al. 2016; Michaletz et al. 2015; Dong et al. 2017, Pau et al. 2018).

Along with T_{air}, VPD also increased linearly with increasing canopy height (Figures 3c, 4e,f). Upper canopies of tropical evergreen species can be particularly susceptible to declines in stomatal conductance due to elevated VPD (Siddiq et al., 2017), yet variation in VPD across tropical canopy height gradients is rarely studied (Rey-Sánchez et al., 2016). The potential decrease in stomatal conductance with increasing VPD has important consequences for CO_2 exchange with the atmosphere of upper canopy leaves.

4.2. Canopy photosynthesis and leaf temperatures

Upper canopies cycle a disproportionate amount of carbon compared to the more shaded middle canopy and understory (Ellsworth and Reich, 1993); therefore, temperature effects on upper canopy foliage can have a disproportionately large effect on whole-forest carbon uptake (Doughty and Goulden, 2008). In our study, upper canopy leaves were exposed to temperatures exceeding 30°C, the mean thermal optimum for photosynthesis measured at this site, an average of 68% of days, and on those days, an average of 3 hours per day. While the T_{opt} sample size was relatively low in our 2016 sampling campaign, a concurrent 2017 study of additional photosynthetic temperature curve measurements from all accessible heights on the same canopy access tower showed mean (±SEM) T_{opt} of *Guarea guidonia* and *Ocotea sintensii* was 31.37 (±0.87)°C (*K. Carter; unpublished data*). T_{opt} was also found to be ~30°C in a nearby Puerto Rican subtropical forest with similar species (Mau et al., 2018). Upper canopy temperatures exceeding photosynthetic thermal optima have been found in tropical forests in Puerto Rico (Mau et al., 2018)), Brazil (Doughty and Goulden, 2008), and Costa Rica (Pau et al., 2018), while shaded leaves in the lower canopies of the Puerto Rican and

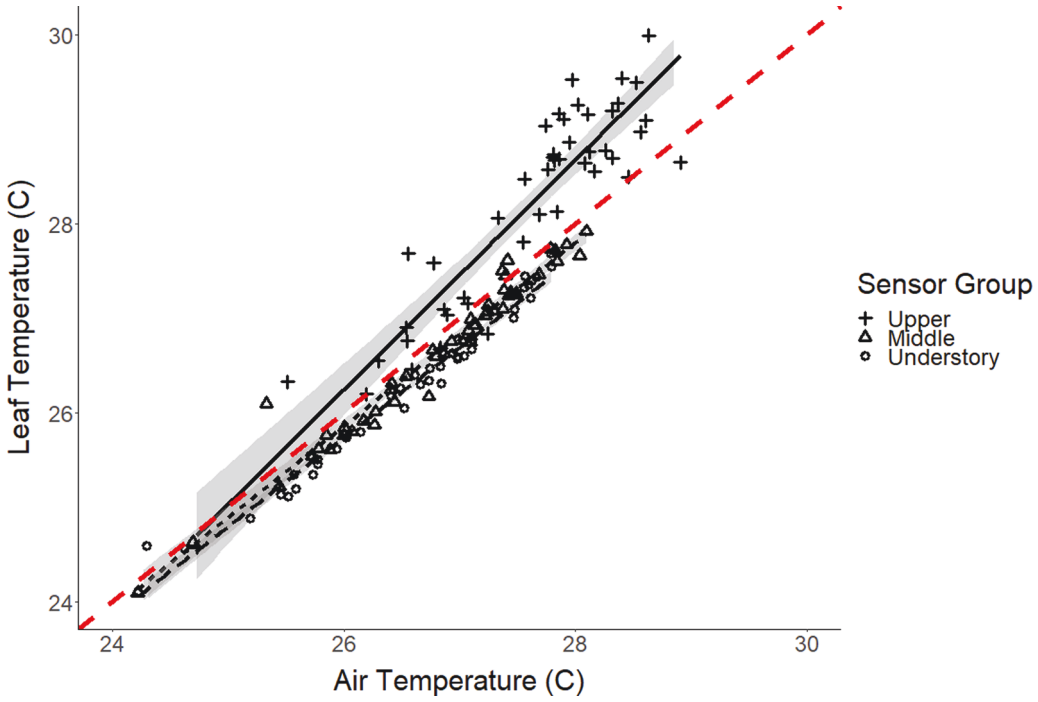

Figure 4. Daily averages of daytime air temperatures versus leaf temperatures along the vertical canopy gradient. The slope of the relationship between T_{leaf} and T_{air} is greater in the upper canopy than either the middle canopy or understory height class ($p < 0.001$) which both fall nearly on the 1:1 line (red dashed line).

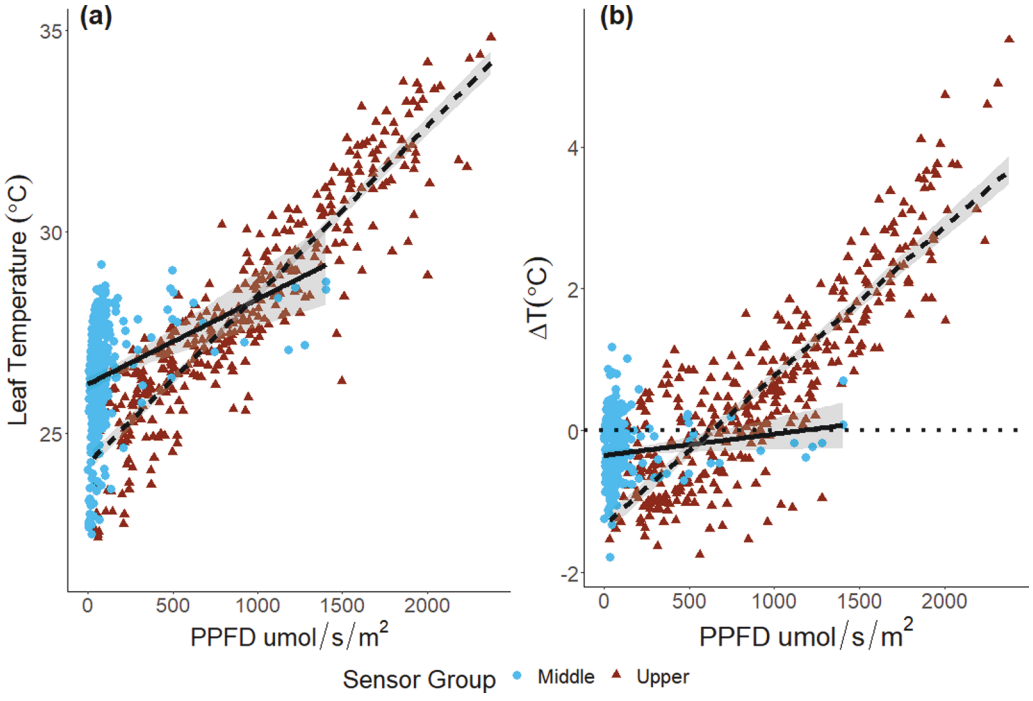

Figure 5. Panel (a) shows the relationships between photosynthetic photon flux density (PPFD) and leaf temperature in both upper (20 m) and middle (10 m) canopy positions. Panel (b) shows the relationships between the difference between leaf temperature and air temperature (ΔT) and PPFD in both upper and middle canopy positions. ANCOVA results indicate that slopes are different between the two canopy positions ($p < 0.001$). The dotted line in Panel (b) represents ΔT= 0. The solid and dashed lines represent slopes for middle and upper canopy, respectively.

Brazilian studies were found to maintain leaf temperatures well below photosynthetic thermal optima (Mau et al., 2018)(Doughty and Goulden, 2008). The drop in photosynthetic productivity when the thermal optima is surpassed is likely due to stomatal closure (Lloyd and Farquhar, 2008; Pau et al., 2018; Tan et al. 2017, Fauset et al. 2019), but could also be attributed to damage to photosynthetic machinery at more extreme temperatures, closer to 40°C (Doughty, 2011). Our results have important implications for carbon balance, because even if the lower canopy positions do not exceed their thermal optima, decreased carbon assimilation in the upper canopy would likely reduce overall tropical forest carbon gain. High temperature-induced stomatal closure in the upper canopy may also have consequences for leaf thermoregulation, as a decline in stomatal conductance can lead to an increase in the difference between leaf and air temperatures (Fauset et al. 2018, 2019). This relationship suggests an important trade-off between thermal stability and the thermal breadth of photosynthesis (Michaletz et al. 2016).m

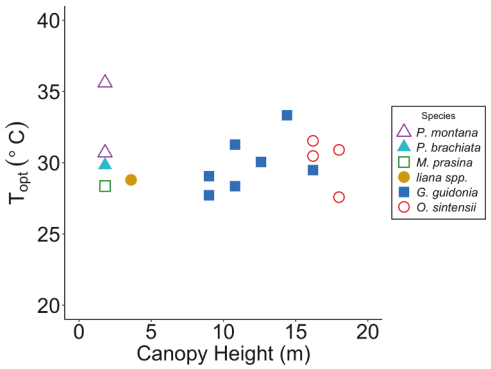

Figure 6. The optimum temperature of photosynthesis (T_{opt}) showed no change across the canopy height gradient. Different colors and symbols represent one palm species (*Prestoea montana*: empty purple triangle), two understory shrub species (*Psychotria brachiata*: filled light blue triangle; *Miconia prasina*: empty green square), two canopy tree species (*Guarea guidonia*: filled dark blue square; *Ocotea sintenisii*: empty red circle), and one unidentified liana species (filled orange circle).

4.3. Leaf thermoregulation strategies differ across the vertical canopy gradient

Differences between T_{leaf} and T_{air} (i.e., ΔT) were near zero in the middle canopy and understory foliage in our study. The upper canopy layer, however, revealed a maximum ΔT of ~5°C (Figure 6b). This magnitude of ΔT is on the lower side compared to what has been reported in other tropical forests. In particular, several studies of understory (Leakey et al. 2003) and upper canopy foliage in tropical forests (Ishida et al. 1999; Dong et al., 2017; (Doughty and Goulden, 2008); Pau et al., 2018) have found maximum ΔT values on the order of ~7 ± 1°C, while some have found ΔT as high as 10°C (Rey-Sánchez et al. 2016) or 18°C (Fauset et al. 2018). Our maximum ΔT values may have been conservative, however, because we employed infrared temperature sensors which were ~50 cm from the leaves rather than direct-contact thermocouples. Additionally, we averaged across 30-minute windows, which also may have dampened high-temperature peaks in our data.

The relationship between T_{leaf} and T_{air} across gradients of space, time, and environmental variables defines a leaf's thermoregulation strategy. When the relationship between T_{leaf} and T_{air} is close to 1:1, this is referred to as poikilothermy (akin to cold-bloodedness in animals), while a slope of zero indicates homeothermy (or homeostasis, akin to warm-bloodedness), where leaf temperatures are constant across the full range of experienced air temperatures (Cavaleri 2020; Michaletz et al. 2016). In reality, leaves are rarely true homeotherms, and when the T_{leaf}: T_{air} slope is between 0 and 1, the term 'limited homeothermy' is useful to describe leaves that are warmer than air at low temperatures and cooler than air under warmer temperatures (Mahan & Upchurch, 1988). The term megathermy is used when leaf temperatures exceed air temperatures, in other words, when the T_{leaf}: T_{air} slope is greater than 1 (Cavaleri 2020, Michaletz et al. 2016).

We found that the thermoregulation strategy of the uppermost layer of foliage in our study was very different from that of the rest of the canopy. Upper canopy leaves that were exposed to the highest light conditions were megathermic (i.e., $T_{leaf} > T_{air}$). Shaded foliage in the lower and mid canopy, on the other hand, revealed poikilothermic behavior (i.e., $T_{leaf} = T_{air}$). Leaves can actively thermoregulate through increased rates of transpiration and evaporative cooling (Bonan, 2008). Some plants can maintain or even increase transpirational cooling at temperatures beyond photosynthetic optima, which can effectively decouple photosynthesis from stomatal conductance (Drake et al., 2018; Urban et al., 2017; Slot et al. 2016; Slot and Winter 2017). We do not find evidence for either homeothermy or limited homeothermy at any canopy height, which suggests an overall limited ability for these tropical trees to thermoregulate. Leaf temperature tracks air temperature tightly throughout most of the canopy, except for the very top where leaf temperatures exceed air temperature. A recent whole-tree chamber study by Drake et al. (2020), also found poikilothermic behavior in eucalyptus canopies, and concluded an overall lack of thermoregulatory capacity. While we do not know how the specific mechanisms of thermoregulation differed across the canopy gradient in our study, we speculate that the shaded leaves maintained poikilothermic behavior by increasing or sustaining stomatal conductance under the full range of air temperatures and radiation conditions experienced throughout the day, while upper canopy leaves likely showed declined stomatal conductance above threshold leaf temperatures and VPD, perhaps conserving leaf water status at the expense of both photosynthetic activity and transpirational cooling.

Forest canopy temperatures can also be influenced by species diversity (Leuzinger and Körner, 2007) via variable stomatal traits or leaf morphology (Fauset et al., 2018). Large size or a high density of stomata can allow for greater stomatal conductance (Beerling et al., 2001; Schymanski et al., 2013) which can, in turn, increase evaporative cooling. A parallel study at this site found both stomatal size and stomatal density to increase from bottom to top of the canopy (*E. Schwartz, unpublished data*). However, this morphological adjustment was apparently not sufficient to avoid megathermy in the upper leaves of our study site. Leaf morphology can also affect evaporative cooling, where smaller or more dissected leaves tend to have thinner boundary layers, allowing for less resistance to diffusion of water vapor (Leigh et al. 2017; Nicotra et al., 2008; Schuepp, 1993). In a tropical forest in Brazil, Fauset et al. (2018) discovered a thermoregulation trade-off whereby species with wider leaves tended to have lower rates of stomatal conductance and higher ΔT. Individual leaf area also tends to decrease with increasing canopy height (Kenzo et al., 2016, Cavaleri et al. 2010), which theoretically could decrease boundary layer thickness and enhance evaporative cooling in the upper canopy. Due to constraints related to equipment and canopy access, we were unable to assess the covariation of species and height, as the areas we were able to measure sometimes contained a mix of species. Future studies including the relationships between leaf morphology, ΔT, and photosynthetic thresholds across species and height gradients would enable a better understanding of the drivers of thermoregulation in tropical forest canopies, as well as improved data to inform modeling efforts.

4.4. Upper canopy as a radiation shield

The foliage in the top layer of the canopy (~20 m) responded to radiation in a very different pattern compared to the foliage in the middle canopy (6-16 m; Fig. 5). Rey-Sánchez et al. (2016) found that T_{leaf} increased with increasing PPFD until it plateaued at close to 500 μmol m^{-2} s^{-1} PPFD. In contrast, we found T_{leaf} to continue increasing linearly with PPFD beyond 2000 μmol m^{-2} s^{-1}, but only in the top layer of leaves (Fig. 5a). The difference between leaf and air temperature (ΔT) increased steeply with PPFD for leaves in the upper canopy, while ΔT was near zero in the middle canopy across the range of PPFD. These results lend support to the idea that tropical canopy leaves exist in two very distinct phases, with very little gradation between: brightly lit and hot, and cooler and shaded, where the carbon uptake of brightly-lit leaves is limited by temperature, while shaded leaves are limited by light (Doughty and Goulden 2008).

The upper canopy could be acting as a radiation shield for the lower portions of the canopy, creating a more shaded and productive environment when enough light is present. Early successional and some mid-successional species develop safety mechanisms such as higher xanthophyll production, which thermally dissipates energy (Adams et al., 2004; Demmig-Adams et al., 1995), and alternate pathways for electron transport that allow them to more quickly acclimate to high light (Kitao et al., 2000; Flexas and Medrano 2002). On the other hand, mid- and later successional species often have lower morphological

plasticity and may not be able to acclimate to the high light environment (Bazzaz, 1979; Kitao et al., 2000; Pearcy et al., 1996). The upper canopy may in fact be acting as a shield to protect the lower canopy to maximize whole-canopy photosynthetic performance (De Frenne et al., 2019). Ishii et al. (2004) found that leaves directly below the leaves in the upper canopy of a closed-canopy temperate forest had higher photosynthetic rates than leaves that were receiving direct sunlight. In our study, this potential 'umbrella effect' would suggest that even when upper canopy leaves were not operating at maximum capacity due to temperatures greater than their thermal optima, the upper canopy shield may allow photosynthetic function to be maintained lower in the canopy. Even though it is possible that the upper leaves may still be photosynthesizing at higher rates than those lower in the canopy due to overall greater metabolic capacity and higher light availability, temperature-induced reduction of GPP in the sun-lit leaves could be partially offset by the lower canopy. As temperatures rise, the shaded leaves may actually increase carbon uptake if they have not yet approached their photosynthetic thermal optima (He et al., 2018). This perspective, together with the large differences we observed in T_{leaf} between the upper canopy (20 m) and just 4 m below (16 m) suggest that higher spatial resolution assessments of the relationship between photosynthesis, T_{leaf}, T_{air}, PPFD, VPD, and stomatal closure in these upper few meters of the canopy could significantly advance our understanding of whole-canopy CO_2 exchange.

5. Conclusions

This work has demonstrated that the uppermost canopy layer of a mature tropical forest was frequently exposed to temperatures above the thermal optimum for photosynthesis, but the remainder of the canopy maintained levels below this critical threshold. While we found both T_{air} and VPD to increase linearly with height, T_{leaf} was neither linear nor constant across canopy height. Rather, there was no difference in T_{leaf} in the lower or mid-canopy, while the top layer of leaves was up to 4°C hotter than the rest of the foliage in the transect. We also found the upper, brightly-lit leaves to exhibit a thermoregulation strategy that was distinct from that of the rest of the shaded foliage. The brightly-lit leaves at the very top layer of the canopy were megathermic, with positive ΔT (i.e., $T_{leaf} > T_{air}$), while ΔT was near zero in the rest of the vertical strata, revealing poikilothermic behavior across the range of air temperatures and radiation experienced by these shaded leaves. We speculate that the upper canopy may act as a radiation shield for the foliage below, where the upper leaves sacrifice photosynthetic gain and evaporative cooling by closing stomata under hot midday conditions, allowing leaf temperatures to rise so the more shaded foliage can maintain stomatal conductance and perform photosynthesis well below thermal optima. As previous studies have suggested, vegetation models should consider the differences in leaf and air temperatures, as leaf temperatures are necessary to accurately simulate plant and ecosystem function. Taken together, our data show large gradients in a range of microclimatic conditions throughout a tropical wet forest canopy, as well as highlight how some variables change linearly through the canopy profile, while others show threshold changes between the uppermost sun-lit leaves and the rest of the shaded foliage below.

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Research Data

Upon acceptance, data and associated metadata will be published in the USDA Forest Service Research Data Archive.

Declaration of Competing Interest

None.

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